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THE DISTRIBUTION OF BUTTERFLIES IN THE MALAY PENINSULA (LEPID.)

By A. Steven Corbet, D.Sc., Ph.D., F.I.C., F.R.E.S.

(*British Museum, Natural History.*)

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Apart from two specialised areas (one in the north-western state of Kedah and the other comprising the east coast islands of the Tioman group), British Malaya constitutes a homogeneous faunistic unit throughout which, subject to the restrictions of altitude and plant association stated below, the Rhopalocerous species are more or less uniformly distributed. Certain species are found only in the mountains, others are confined to the plains and a number occur at all elevations. A few species which appear to be strictly montane in Malaya proper [1] inhabit the plains in north Kedah. Most of the species are restricted to one or two of the three principal plant associations. These comprise primary forest, secondary growth in various stages of reversion to forest, which, in Malaya, is practically confined to the plains, and the coastal mangrove swamps, which often extend inland to a depth of several miles and occur more frequently on the west coast than on the east.

The equatorial belt is characterised by high temperature and humidity and heavy rainfall and these conditions favour a rich flora and fauna. With the butterflies, one brood succeeds another throughout the year, and the species are in flight continuously although, in the Malay Peninsula, some species are more abundant between December and May than during the remaining months of the year. There is no seasonal differentiation in Malaya proper such as occurs in monsoon areas but, with a few species, the "dry-season form" occurs as a rare aberration.

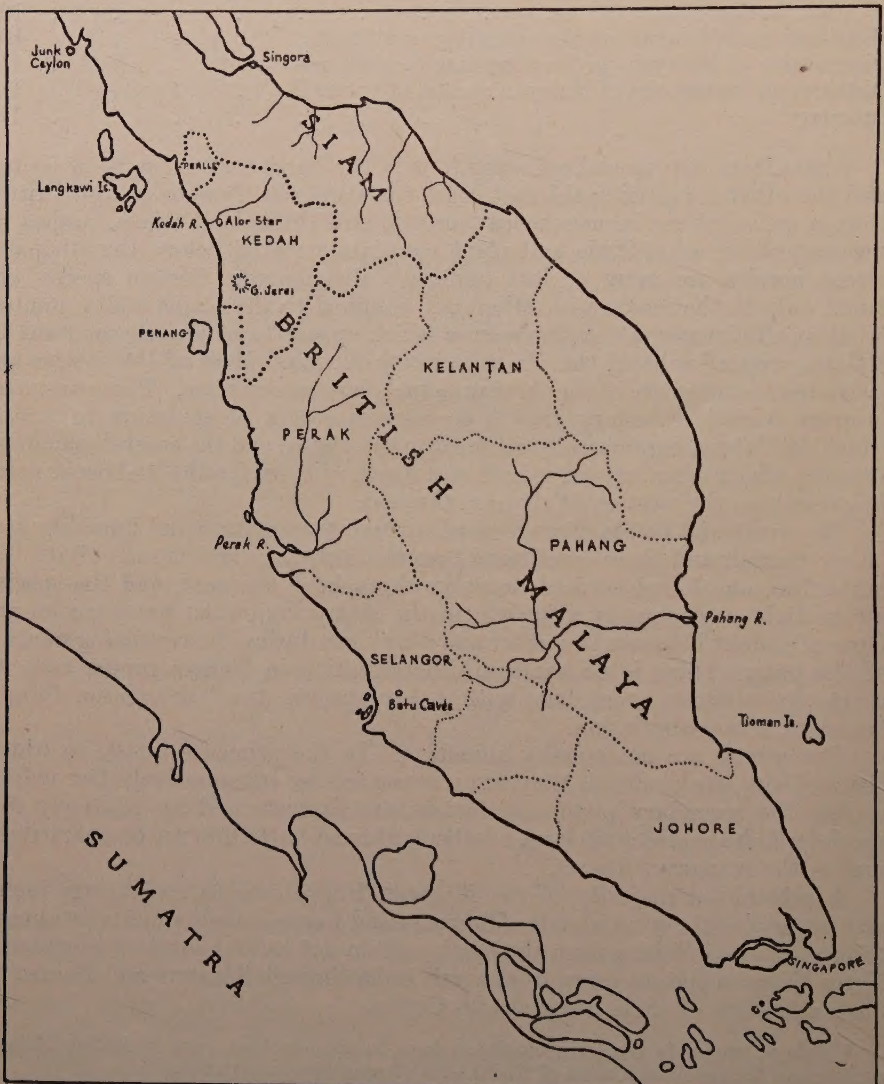
The species are not equally abundant. In the primeval forest, to which the majority are confined, they are represented by comparatively few individuals; the secondary plant associations are characterised by relatively few species which are present in large numbers, whereas butterflies are comparatively rare in the mangrove forests.

A substantial majority of the Malayan Rhopalocerous species are found also in the neighbouring islands of Sumatra and Borneo, while a minority appear to have reached Malaya from the north and do not extend south of Singapore. Many Malayan species range from north India through Sumatra and Borneo to Java and some of these occur also in Ceylon.

[1] Malaya proper is the term employed here to connote that part of British Malaya exclusive of the specialised areas of Kedah and Tioman mentioned above.

Geographical differentiation of species and subspecies in Kedah and the Tioman Islands.

It is well established that, as late as the Pleistocene Age, the present Malay Peninsula, the Large Sunda Islands (Sumatra, Borneo and Java) and their satellite islands, and almost certainly Palawan and Balabac also, were united to form a large continent which has been termed Sundaland (Molengraaf, 1921, *Geog. J.* **57** : 101). Most of this ancient land now lies beneath the sea and constitutes the Sunda Shelf, the depth of which nowhere exceeds 100 fathoms and is usually much less. It seems clear that Java was the first major island to be isolated, while the final separation of the Malay Peninsula from Sumatra is much more recent. What now remains of Sundaland is known as Malaysia



and comprises the three fairly clearly defined zoo-geographical sub-regions of Java, Neomalaya (consisting of the Malay Peninsula, Sumatra and Borneo), and Paramalaya, the last-named constituting the islands off the west coast of Sumatra.

The position regarding the land connection between Sundaland and the asiatic mainland is more obscure, but further light has been thrown on the subject by a study of the distribution of the Malayan Rhopalocera.

Of the 924 species of butterflies recorded from the Malay Peninsula, 35 are known only from a small area in the north-west corner of British Malaya which comprises the small northern state of Perlis, that part of Kedah north of the Kedah River, and the Langkawi Islands, which are situated 14 miles from the Kedah coast (fig. 1). In order to avoid constant repetition I propose in this paper to refer to this specialised area as " Kedawi." Of these 35 " endemic " " Kedawi " species,[2] of which three-quarters do not otherwise extend into Malaysia, 28 have been recorded from the Langkawi Islands and 20 from the north Kedah mainland and Perlis. The majority of these species are not rare stragglers in " Kedawi " but are well-established insects which, in many instances, are not uncommon. The subjoined Table I gives the extra-Malayan

TABLE I.

Distribution of the Malayan species of Rhopalocera outside the Malay Peninsula.

Family	Total in family	Species found also in				Endemic (not north of Mergui or south of Singapore)
		Ceylon	Burma, north of Mergui [3]	Sumatra and/or Borneo [4]	Java	
PAPILIONIDAE .	45	11 (24·4)	34 (75·6)	40 (88·9)	29 (64·4)	—
PIERIDAE . .	48	15 (31·3)	38 (79·2)	39 (81·2)	27 (56·6)	—
DANAIDAE .	39	9 (22·5)	25 (62·5)	31 (79·4)	26 (65·0)	1 (2·5)
SATYRIDAE .	53	4 (7·6)	35 (66·0)	41 (77·3)	25 (47·2)	—
AMATHUSIIDAE .	26	— (—)	12 (46·2)	21 (80·8)	8 (30·8)	2 (7·7)
NYMPHALIDAE .	144	27 (18·6)	99 (68·9)	124 (85·4)	92 (63·4)	—
LIBYTHEIDAE .	2	1 (50·0)	2 (100·0)	2 (100·0)	2 (100·0)	—
RIODINIDAE .	15	— (—)	10 (33·3)	12 (80·0)	7 (46·7)	—
LYCAENIDAE .	337	47 (13·9)	215 (63·6)	286 (84·8)	167 (49·4)	16 (4·7)
HESPERIIDAE .	215	34 (15·8)	166 (77·2)	175 (81·4)	105 (48·8)	1 (0·5)
Total .	924	148 (16·0)	636 (68·8)	771 (83·4)	488 (52·8)	20 (2·2)

The figures calculated on a percentage basis are shown in brackets.

distribution of the total Malayan species as far as Ceylon, Burma, Sumatra, Borneo and Java are concerned; Table II shows the same extra-Malayan

[2] The species here considered as " endemic " are, of course, only endemic in " Kedawi " with respect to British Malaya as a whole.

[3] For the purpose of this paper, species are regarded as Burmese in habitat only if found north of Mergui. Such a boundary precludes a few Malaysian species which have reached Victoria Point in southern Burma from being considered as Burmese.

[4] The Rhopalocerous fauna of Sumatra and Borneo is so much less well known than those of Burma, Malaya and Java that it appears preferable to consider them together, for it is highly probable that almost all the species found in two of the large components of Neomalaya will be discovered eventually in the third.

TABLE II.

Distribution of "Kedawi" "endemic" species outside the Malay Peninsula.

Total species	Species found also in			
	Ceylon	Burma, north of Mergui	Sumatra and/or Borneo	Java
35	8 (22·9)	33 [5] (94·3)	13 (37·1)	5 (14·3)

The figures calculated on a percentage basis are shown in brackets.

distribution for the "endemic" "Kedawi" species, and it is clear that these latter forms are distributed in a different proportion outside of Malaya.

From the above tables it is seen that, whereas over 80 per cent. of the total Malayan species are found also in Sumatra and/or Borneo and a little over two-thirds in Burma, in the case of the "endemic" "Kedawi" species, 95 per cent. occur also in Burma, while little more than one-third are known from Sumatra and/or Borneo.

It is a curious fact that several species which are more or less restricted to "Kedawi" as far as British Malaya is concerned, occur also in Sumatra and/or Borneo: such species are *Papilio aristeus* Stoll, *P. megarus* Westw., *Cepora nerissa* (F.), *Danaus similis* (L.), *Amblypodia anita* Hew., *Ticherra acte* (Mre.), *Marmessus scudderii* (Doh.), *Plastingia fuscicornis* (El. & Edw.), *P. noemi* Nic. and *Baoris unicolor* Mre.; one Kedah species, *Yoma sabina* (Cr.), is unknown from Sumatra and Borneo but occurs in Java.

A number of species common to both Malaya proper and "Kedawi" occur in the latter area as distinct geographical races. Leaving aside the "endemic" "Kedawi" species dealt with in Table II, of the 200 species examined by me from the Langkawi Islands, 36 are there represented by distinct subspecies: of the 117 species from the north Kedah mainland known to me, 9 occur as races distinct from the form from Malaya proper; one butterfly, *Lebadea martha* (F.), has well-differentiated races on the Langkawi Islands, on the mainland of north Kedah and in Malaya proper.

The present position regarding the "Kedawi" species and subspecies is summarised in the following table, in which the figures in brackets represent percentages.

	Total species known to me	Species confined to "Kedawi"	Subspecies distinct from those from Malaya proper	Subspecies identical with those from Malaya proper
Langkawi Islands . .	228 (100·0)	28 (12·3)	36 (15·8)	164 (71·9)
North Kedah mainland .	137 (100·0)	20 (14·6)	9 (7·3)	108 (78·1)
Whole of "Kedawi" .	276 (100·0)	35 (12·7)	41 (14·8)	200 (72·5)

The only other part of British Malaya inhabited by species which are not found throughout the Peninsula and by species present as well-differentiated

[5] Including *Ariadne specularia* (Fruh.) and *Miletus archilochus* (Fruh.), which extend into Indo-China, but are not known from Burma.

races is the east coast islands of the Tioman group. These islands lie off the coast of the states of Pahang and Johore and are distant some 27 miles from the nearest point on the mainland. Of the 52 Tioman species examined by me,[6] 5 are not otherwise known from Malaya and 17 are represented in Tioman Island by distinct subspecies. In percentages :—

	Species confined to Tioman Is.	Subspecies distinct from those from Malaya proper	Subspecies identical with those from Malaya proper
Tioman Islands . . .	9·6	32·7	57·7

Thus, it will be seen that the Rhopalocerous fauna of the Tioman Islands is even more highly differentiated than that of " Kedawi," the differences between the two being statistically significant as shown by the χ^2 test.[7]

	Percentage species and subspecies confined to the area	Percentage subspecies identical with those from Malaya proper	Total
Whole of " Kedawi " . .	27·5	72·5	100·0
Tioman Islands . . .	42·3	57·7	100·0
χ^2	7·97	3·02	10·99
$n = 1$ $P < 0{\cdot}01$	Difference highly significant		

There are no other areas in British Malaya showing a specialised fauna in any way comparable with those of " Kedawi " and the Tioman Islands. Singapore Island has a single resident species, *Pieris canidia* (L.), not found elsewhere in Malaya, *Tenaris horsfieldii* (Swains.) appears not to extend farther north than Johore, and the Singapore race of *Polyura hebe* (Btlr.) is distinct from that of the mainland. These differences, however, are slight, although Singapore Island shares a few species with Tioman Island and it is probable that a number of rather weak races of Lycaenidae could be discovered in Singapore were sufficient material available for study.

[6] Leaving aside *Euploea brookei* (Mre.) and *E. ochsenheimeri* Luc., which probably represent well-differentiated subspecies of *E. modesta* Bltr. and *E. midamus* (L.) respectively, but regarding which no definite statement can be made pending a revision of the genus *Euploea* F.

[7] In this test of significance, χ^2 is calculated from the relation $\chi^2 = S\left(\frac{x^2}{m}\right)$, where m and $(m + x)$ are the expected and observed values respectively. The probability P of the difference between the observed and expected values occurring by chance is found by entering a table for χ^2 at the appropriate value for n, n being the number of degrees of freedom which, in the present examples, corresponds to the number of independent variables. On the usual $P = 0{\cdot}05$ level of significance, differences are regarded as statistically significant when they can occur by chance not more frequently than once in twenty times. In all the examples in the present paper in which significant differences between observed and expected values are shown by the χ^2 test, P is less than 0·01, indicating that these differences could occur by chance less than once in 100 times (*vide* Fisher, 1934, *Statistical Methods for Research Workers* : 80).

From the above figures, it may be fairly concluded that the past history of the land area in the north-west of British Malaya which has here been termed " Kedawi " has not been identical with that of Malaya proper. The abrupt change witnessed in the Rhopalocerous fauna on proceeding north through Kedah suggests that, in comparatively recent times, there existed (and may still exist) somewhere in the neighbourhood of the Kedah River a natural barrier obstructing the passage of butterflies between south Burma and Malaya proper.

This discontinuity in distribution is not confined to the Rhopalocera. Ridley (1911, *J. Straits Br. R. asiat. Soc.* **59** : 15, 27) found the flora of the Siamese Malay States to be quite distinct from that of Malaya proper, many characteristic Malayan genera being absent, and he placed the boundary line near Alor Star on the Kedah River. The flora of the granite massif known as Kedah Peak (Gunong Jerei), in south Kedah, was found to pertain to Malaya proper and the same case obtains with regard to the butterfly fauna.[8] Ridley concluded that, in the not very remote past, the Malay Peninsula was separated from the mainland of Asia where Kedah now stands by an arm of the sea. Moreover, Gerini (1909, *Researches on Ptolemy's Geography of Eastern Asia* : 78–80) claims there is geological evidence to show that the land between Kedah and Singora (latitude 6°–7° N.) is an old sea bed.

Attractive as is the hypothesis of a former sea channel between Alor Star and the Gulf of Siam, there are difficulties in the way of accepting it as a complete explanation of the specialised flora and fauna of " Kedawi." In the first place, the topography of this region suggests that any such sea channel must have been situated farther north than Alor Star. Further, the geological formation of " Kedawi " is remarkable for a high proportion of limestone, although isolated limestone outcrops extend along the western side of the Peninsula as far south as the Batu Caves in Selangor[9]; in " Kedawi," the climate also is somewhat differentiated from that of Malaya proper and these factors must all be taken into account.

From the paper by Dr. Zeuner which follows, it will be seen that the probable explanation of the differentiated flora and fauna of " Kedawi " is that, while Malaya proper has undoubtedly been separated from the asiatic mainlain since the present species of butterflies came into being, it appears that this separation occurred north of Kedah, but the southward spread of certain immigrant species and subspecies from the present Siamese Malay States has been prevented by a barrier which is largely climatic. Although the total rainfall in " Kedawi " is not significantly less than in Malaya proper, the rainfall during the driest month is considerably less than that during the wettest month of the year, and in this important respect the climate of " Kedawi " approaches that of Burma. This effect of a dry season, which is accentuated on a limestone formation, appears to be an important factor in maintaining

[8] For information regarding the butterflies of Kedah Peak (altitude 3978 feet), I am indebted to Mr. H. M. Pendlebury, Director F.M.S. Museums, who visited the mountain in 1928.

[9] Quite recently, Henderson (1939, *J. Malay. Br. R. asiat. Soc.* **17** : 24) has found that of 64 or 65 plant species recorded as confined to the limestone outcrops in the Malay Peninsula but with a distribution outside it, 50 are known only from localities north of Malaya on the asiatic mainland. The bulk of these northern plants, moreover, do not extend far into the Peninsula, most of them being confined to the Langkawi Islands, Kedah and Perlis. Mr. H. M. Pendlebury has reported (*in litt.* 26.ii.1941) that two " Kedawi " species of butterflies, *Papilio megarus* Godt. and *Everes potanini* (Alph.), have recently been taken by Mr. G. C. Stubbs round the limestone cliffs near Ipoh in Perak.

the distinctness of the "Kedawi" flora and fauna. To a lesser extent, the east coast of Malaya exhibits the same phenomenon of a dry seasonal effect (*vide* fig. 3 in the following paper), and it would be interesting to ascertain whether there is any tendency towards the formation of local races among the butterfly species which are most susceptible to such influences.

Relation between abundance of Malayan species and their extra-Malayan distribution.

The view that the most widely distributed species of plants and animals are the most abundant has been advanced a number of times (although I do not recollect having seen any quantitative evidence to this effect), and it is instructive to test this hypothesis with regard to the Malayan species of butterflies.

Table I gives the number of Malayan species found also in Ceylon, Burma north of Mergui, Sumatra and/or Borneo, and Java and, from the data which served for the compilation of this table, it is possible to separate the species into the following four distribution groups :—

(*a*) those species found north of Mergui but not south of Singapore (termed "northern" species);
(*b*) those found in Sumatra and Borneo, and with some species in Java also, but not north of Mergui (termed "southern" species);
(*c*) those ranging from Burma north of Mergui to Sumatra, Borneo and Java;
(*d*) as in (*c*) but found in Ceylon also.

In Table III the species found in these distribution groups are classified according to relative abundance. The figures for the abundance groups are based on the results of my own collecting during 5 years residence in British Malaya, such collecting being carried out as often as possible at all elevations and in all three plant associations.

Although it might be suggested that the ratio (specimens collected)/(number of species) should be taken as a measure of relative abundance, it appeared preferable to divide the species into groups according to abundance rather than to use the actual numbers collected. In this way, some allowance is made for species which occur in small colonies, but a further and more cogent reason for grouping is that, as little useful purpose was served by continued collecting of very common species in Malaya, such collecting was discontinued in each locality once a representative series had been obtained. Thus, with species in which more than 24 specimens were collected, in most cases larger numbers could have been obtained had attempts been made to catch all the butterflies seen. Nevertheless, even with the very common species, the numbers collected are still roughly proportional to the numbers seen.

In Table III the species are divided into five groups according to abundance : (*a*) very common species in which more than 24 specimens were obtained; (*b*) common species with 10 to 24 specimens, (*c*) less common species with 5 to 9 specimens, (*d*) rare species with 1 to 4 specimens, (*e*) very rare species of which no examples were caught. The *coefficient of abundance* in the last column in each row is calculated from the formula :

$$\frac{5\,(a) + 4\,(b) + 3\,(c) + 2\,(d) + (e)}{n},$$

n being the total number of species pertaining to the distribution group.

TABLE III.

Relative abundance of species according to distribution groups.

Distribution group	Total number of species (n)	Number of species in each frequency group (*a*)	(*b*)	(*c*)	(*d*)	(*e*)	Coefficient of abundance
				PAPILIONIDAE and PIERIDAE.			
Northern	11	—	2	1	4	4	2·09
Southern	21	5	4	3	7	2	3·14
Burma to Java	24	9	7	2	3	3	3·67
Ceylon to Java	21	15	3	1	1	1	4·43
				NYMPHALIDAE group (DANAIDAE to RIODINIDAE).			
Northern	35	4	4	4	11	12	2·34
Southern	86	14	13	14	18	27	2·64
Burma to Java	76	22	17	4	28	5	3·30
Ceylon to Burma	34	14	10	2	5	3	3·79
				LYCAENIDAE.			
Northern	20	—	1	2	8	9	1·75
Southern	92	3	11	9	29	40	2·00
Burma to Java	93	11	13	15	24	30	2·47
Ceylon to Java	42	10	11	12	6	3	3·45
				HESPERIIDAE.			
Northern	33	—	1	4	10	18	1·64
Southern	44	—	3	4	15	22	1·73
Burma to Java	67	7	7	7	21	25	2·25
Ceylon to Java	23	1	4	9	6	3	2·74
				Whole of Rhopalocera.			
Northern	99	4	8	11	33	43	1·96
Southern	243	22	31	30	69	91	2·28
Burma to Java	260	49	44	28	76	63	2·77
Ceylon to Java	120	40	28	24	18	10	3·58

It will be seen that, with all the four groups of families and with the total species, the " northern " species are the rarest, next in order come the " southern " species, then those distributed from Burma to Java, while the most widely ranging species (Ceylon to Java) are the most abundant. The " northern " species comprise the smallest group numerically, a not unexpected result which emphasises Malaya's much closer relationship with Sumatra and Borneo than with Burma.

Distribution of Malayan species according to altitude.

A range of mountains, which in general attains a height of about 4000 feet, runs from Kedah to north Johore, and there are many peaks, mostly on the main range, which reach altitudes up to 7000 feet. There are a few smaller parallel chains in Perak and Pahang.

Rather more than half the Malayan species of butterflies are confined to the plains, about a third of this number are found only on the hills and between a quarter and one-fifth of the total occur on both sides of the 2500-feet line which, for the purpose of this paper, is taken as the upper and lower limit

respectively for the plains and montane species. At this altitude the mean temperature is just over 70° F., as against 80° on the plains, and the annual rainfall exceeds the 90–100 inches of the plains. Here, also, differences in plant-life are apparent to the casual observer, and this division has the further advantage of practically restricting all the *Delias* species (PIERIDAE), other than *D. hyparete* (L.), to the montane group.

TABLE IV.

Distribution of Malayan Rhopalocera according to altitude.

	M Montane	P Plains	U All elevations	Total
PAPILIONIDAE and PIERIDAE . .	17	35	34	86
NYMPHALIDAE group	34	130	89	253
LYCAENIDAE	59	197	68	324
HESPERIIDAE	25	137	30	192
Total	135	499	221	855

The totals are given in Table IV: species confined to "Kedawi" and to the Tioman Islands are excluded as they are not strictly comparable with the truly Malayan species from Malaya proper, and a few anomalous species (e.g. *Pieris canidia* (L.), which is confined to Singapore and is probably a comparatively recent introduction from south-east China), and those known only from one or two examples without sufficiently detailed data are also omitted.[10]

Of the species found only above or below the 2500-feet line included in the above table, 21·3 per cent. are montane and 78·7 per cent. pertain to the plains.

Although detailed information is now available regarding the distribution of most of the Malayan Rhopalocera, in two groups, the extensive genus *Arhopala* Bsdv. (LYCAENIDAE) and the family HESPERIIDAE, many of the species are extremely rare and the Malayan records often rest on a single specimen. As much more collecting is carried out below 2500 feet than above this altitude, it is evident that records of very rare species must show a bias towards the plains and, for this reason, it appeared preferable to omit the *Arhopala* and HESPERIIDAE from the calculation of the montane/plains ratio. The data thus amended are given in Table V.

The montane and plains species included in Table V occur in the proportions 25·1 per cent. and 74·9 per cent. respectively and this estimate is unlikely to be modified much by further discoveries. The χ^2 test shows there is no significant difference between the montane/plains ratio for the LYCAENIDAE (excluding

[10] The species thus excluded are: *Pieris canidia* (L.), *P. napi* (L.), *Euploea core* (Cr.), *Ypthima philomela* (L.), *Charaxes marmax* Westw., *Libythea narina* Godt., *Mahathala ameria* (Hew.), *Arhopala johoreana* Cbt., *A. malayana* B. Bkr., *A. tropaea* Cbt., *A. kurzi* (Dist.), *A. agamemnon* Cbt., *A. corinda* (Hew.), *A. cardoni* Cbt., *A. epimete* (Stgr.), *A. ammon* (Hew.), *Catapaecilma elegans* (H. Drc.), *Ritra aurea* (H. Drc.), *Poritia hewitsoni* Mre., *Hasora borneensis* El. & Edw., *Bibasis jaina* (Mre.), *B. gomata* (Mre.), *Choaspes furcata* Evans, *Celaenorrhinus nigricans* (Nic.), *Coladenia agni* (Nic.), *Koruthaialos kerala* Nic., *Erionota sybirita* (Hew.), *Plastingia flavia* Stgr., *Zela zeus* Nic., *Halpe sikkima* Mre., *Iton watsonii* (Nic.).

Table V.

Distribution of Malayan Rhopalocera according to altitude (excluding *Arhopala* and Hesperiidae).

	M Montane	P Plains	U All elevations	Total
Papilionidae and Pieridae	17	35	34	86
Nymphalidae group	34	130	89	253
Lycaenidae (excluding *Arhopala*)	50	136	57	243
Total	101	301	180	582

Arhopala) and that for the combined Papilionidae, Pieridae and families of the Nymphalidae group.

	Percentages		
	Montane	Plains	Total
(*a*) Papilionidae, Pieridae and Nymphalidae group	23·6	76·4	100·0
(*b*) Lycaenidae (excluding *Arhopala*)	26·9	73·1	100·0
χ^2	0·461	0·142	0·603

$n = 1$
P between 0·50 and 0·30
Difference between (*a*) and (*b*) not significant

If the "northern" and "southern" species are arranged in groups according to their occurrence above or below or on both sides of the 2500-feet altitude line, it is found that the proportion of M (montane), P (plains) and U (all elevations) species among the southern species is not significantly different from that of the total Malayan species as given in Table V. On the other hand, the northern species occur in quite a different proportion, the montane species comprising nearly two-thirds of the total (Table VI). As before, the species confined to "Kedawi" or to the Tioman Islands, together with the few anomalies and rare species with insufficient data (*vide* page 109), are omitted from the table and the genus *Arhopala* and the family Hesperiidae are also left out of consideration.

Reduced to round numbers, it may be stated that, of the total Malayan Rhopalocerous species under consideration which are confined either to the hills or the plains, 25 per cent. are montane as against 75 per cent. on the plains and the same ratio obtains with the "southern" species. In the case of the "northern" species, 72 per cent. are montane as against 28 per cent. on the plains.

It has been shown already that, in Malaya proper, the "northern" species are consistently rarer than the "southern" species and it is evident that these insects of northern origin are the more recent arrivals, for, unless one postulates the highly improbable hypothesis that these same species, or a proportion of them, have already been established and subsequently become

extinct in the Large Sunda Islands, one must assume that they reached Malaya after the final severance of the Peninsula from Sumatra.

It may be mentioned that only 12 of the 45 " northern " species in Table VI are listed in Distant, 1886, *Rhopalocera Malayana*, as against 81 of the 154 " southern " species, but this is hardly a legitimate comparison as the montane

TABLE VI.

Distribution of " northern " and " southern " species according to altitude.

	" Northern " species				" Southern " species			
	M Montane	P Plains	U All elevations	Total	M Montane	P Plains	U All elevations	Total
PAPILIONIDAE and PIERIDAE . .	6	1	1	8	7	9	5	21
NYMPHALIDAE group.	15	6	4	25	4	35	35	74
LYCAENIDAE (excluding *Arhopala*) .	7	4	1	12	14	35	10	59
Total . .	28	11	6	45	25	79	50	154
(*a*) Above as percentages . .	62·2	24·5	13·3	100·0	16·2	51·3	32·5	100·0
(*b*) Table V totals as percentages .	17·4	51·7	30·9	100·0	17·4	51·7	30·9	100·0
χ^2 . . .	115·3	143·1	246·5	504·9	0·083	0·003	0·082	0·168
n . . .	2				2			
P . . .	<0·01				Between 0·95 and 0·90			
Difference between (*a*) and (*b*) . .	Highly significant				Not significant			

TABLE VII.

Relative abundance of " northern " and " southern " species with respect to altitude (excluding *Arhopala* and HESPERIIDAE).

	Totals	Number of species in each frequency group					Coefficient of abundance
		(*a*)	(*b*)	(*c*)	(*d*)	(*e*)	
Northern species :							
Montane . .	28	—	4	3	4	17	1·78
Plains . .	11	2	1	—	4	4	2·36
Total . .	39	2	5	3	8	21	1·95
Southern species :							
Montane . .	25	2	3	4	12	4	2·48
Plains . .	79	9	6	11	24	29	2·26
Total . .	104	11	9	15	36	33	2·32

species predominate in the "northern" group and there was little collecting above 2500 feet in Distant's day. Nevertheless, a comparison of the total specimens collected by me for the "northern" and "southern" species found above the 2500-feet line shows the northern forms definitely to be the rarer (Table VII).

If the Malayan Rhopalocera (other than *Arhopala* and HESPERIIDAE) are grouped into "montane", "plains" and "all elevations" (using 2500 feet as the dividing line as before), it is found that while two-thirds of the species in each altitude group occur also in Burma north of Mergui, a smaller proportion of the montane forms and a much greater proportion of the "all elevation" species extend to Sumatra, Borneo and Java (*vide* Table VIII).

TABLE VIII.

Distribution of Malayan altitude groups outside of the Malay Peninsula (excluding *Arhopala* and HESPERIIDAE).

	Total	Species found also in			
		Ceylon	Burma, north of Mergui	Sumatra and/or Borneo	Java
Montane	101	7 (6·9)	68 (67·3)	67 (66·3)	37 (36·6)
Plains	301	61 (20·3)	205 (68·1)	262 (87·0)	180 (59·8)
All elevations	181	36 (19·9)	122 (67·4)	177 (97·8)	134 (74·0)

The figures calculated on a percentage basis are shown in brackets.

Among the few species which are more or less strictly montane in Malaya proper and yet found on the plains in "Kedawi" may be mentioned *Papilio mahadeva* Mre., *Euploea leucostictos* (Gmel.), *Neptis harita* Mre., *Euthalia julii* (Lesson), *Celastrina cyma* Tox., *Arhopala ijauensis* B.Bkr. and *A. bazalus* (Hew.). It is, perhaps, worthy of note, that one or two species show a difference in habit in "Kedawi" and in Malaya proper. *Arhopala ijauensis* is essentially a primary forest species in Malaya and yet occurs in open secondary growth in "Kedawi"; the same difference in habit is shown by *Papilio coon* F. and *Lebadea martha* (F.).

Distribution of Malayan species according to plant association.

The primary forest is inhabited by a large number of species with a relatively small number of individuals, while the secondary plant associations are characterised by a comparatively small number of species which are each represented by numerous individuals. So much is apparent to every serious collector of Rhopalocera in the Malay Peninsula, but an examination of the available data shows that the secondary growth species are differentiated in other ways.

According to a list prepared mainly on the basis of my own collecting, but supplemented by evidence from other collectors, and excluding the species restricted to the specialised areas of "Kedawi" and the Tioman Island group, 117 species of Malayan butterflies can be regarded as pertaining to secondary growth associations; a few of these occur also in primary forest and others may be found rarely on the forest edge. The extra-Malayan distribution of these

secondary growth species is given in Table IX, where the terms "northern" and "southern" are applied as previously. About one-half of the 10 species grouped under "other distributions" are found in Burma, Sumatra and Borneo, and most of the remainder occur from Java, Sumatra and Borneo to China although absent from Burma. The last two columns in Table IX give the extra-Malayan distribution for the whole of the Malayan Rhopalocera based on the data in Table III.

TABLE IX.

Extra-Malayan distribution of secondary growth species.

	Secondary growth species		Whole of Malayan Rhopalocera	
	Actual numbers.	Percentages	Actual numbers.	Percentages
Northern	7	6·0	99	10·7
Southern	6	5·1	243	26·3
Burma to Java	35	29·9	260	28·1
Ceylon to Java	59	50·4	120	13·0
Other distributions	10	8·6	202	21·9
Total	117	100·0	924	100·0

It is apparent from Table IX that the secondary growth butterflies in Malaya are mostly widespread species, half of which are found from Ceylon to Burma, through Neomalaya, to Java; compare this with the 13 per cent. of the whole of the Malayan Rhopalocera with the same range.

It is interesting to note that, as far as the butterfly fauna is concerned, the Krakatau Islands in the Sunda Straits have been recolonised very largely by secondary growth species which are distributed from Ceylon to Burma, Neomalaya and Java. These islands were the scene of a catastrophic volcanic eruption in 1883, when they were covered with hot ashes and pumice to a depth of over a hundred feet and the vegetation was entirely destroyed. By 1928, 30 species of butterflies were known from the islands but, of these, 6 Hesperiids must be left out of consideration as their identification is uncertain. The remaining 24 Krakatau species fall into distribution groups as under :—

Northern species	0
Southern species	4
Burma–Java species	5
Ceylon–Java species	15
Total	24

All of the Krakatau species occur in both the neighbouring islands of Sumatra and Java.

The reversion of cleared land to primary forest in the equatorial belt takes place in a series of stages in which one plant succession follows another. As the degree of shading increases, certain sun-loving plant species characteristic of the earlier stages disappear and are replaced by species preferring shade. It is evident that, before the present large-scale interference with nature by man in

Malaysia, areas of secondary growth at more or less the same stage of development, and so harbouring the same plant species, must have been few and far between. The continued existence of certain species of Lepidoptera whose larvae feed on plants confined to the secondary growth association during its early stages would only be assured if such insects were able to move on from one cleared area to others at the same or at a slightly earlier stage in the reversion process when the food-plants disappeared or when limited supplies were exhausted. It may well be that the phenomenon of migration in Lepidoptera owes its origin to this continual necessity on the part of secondary growth butterflies to discover and to colonise new areas of secondary plant associations at certain stages of development, for the majority of the Indo-Malayan species of butterflies listed as migratory by Williams (1930, *Migration of Butterflies*) are secondary growth species in Malaya having an extra-territorial distribution at least from Ceylon to Burma, through Neomalaya, to Java.

TABLE X.

Relative abundance of Malayan Rhopalocera according to families.

	(i) Total species	(ii) Total specimens collected	Ratio (ii)/(i)	Number of species in each frequency group					Coefficient of abundance.
				(a)	(b)	(c)	(d)	(e)	
PIERIDAE .	48	1326	27·6	19	13	2	6	8	3·60
DANAIDAE .	39	817	20·9	12	7	1	10	9	3·07
PAPILIONIDAE .	45	724	16·1	10	9	7	12	7	3·07
NYMPHALIDAE .	144	1956	13·6	34	25	21	38	26	3·03
SATYRIDAE .	53	677	12·7	8	13	7	15	10	2·88
LYCAENIDAE .	337	2274	6·8	25	38	42	94	138	2·16
RIODINIDAE .	15	87	5·8	—	3	3	7	2	2·47
AMATHUSIIDAE.	26	134	5·2	1	4	1	10	10	2·08
LIBYTHEIDAE .	2	10	5·0	—	1	—	—	1	2·50
HESPERIIDAE .	215	1026	4·8	10	18	26	68	93	2·00
LYCAENIDAE subfamilies arranged separately.									
LYCAENINAE .	91	1403	15·4	17	20	18	21	15	3·03
MILETINAE .	27	181	6·7	2	2	5	8	10	2·18
THECLINAE .	201	678	3·4	6	16	19	58	102	1·83
PORITIINAE .	17	11	0·6	—	—	—	6	11	1·35

Of certain families of Rhopalocera, notably PIERIDAE, DANAIDAE and the subfamily LYCAENINAE, a relatively large proportion of the species favour secondary plant associations rather than primary forest. On the other hand, in the AMATHUSIIDAE, HESPERIIDAE and the subfamily THECLINAE, most of the species are true denizens of the forest. An estimate of the relative abundance of the Malayan butterfly species by families based on the results of my collecting from 1927 to 1932 shows the PIERIDAE and DANAIDAE to be the most abundant, and the AMATHUSIIDAE, HESPERIIDAE and THECLINAE to be the rarest (Table X). It will be seen that, except for the very small families LIBYTHEIDAE and RIODINIDAE, the families follow the same order whether arranged according to the coefficient of abundance or the ratio (specimens captured)/(species in family).

It is hardly a matter for surprise that there is a paucity of data regarding the

distribution of butterflies in the crocodile-infested mangrove forests which fringe the more sheltered parts of the Malayan coast. Few butterflies were seen during my few visits. There are, however, a few species of Malayan butterflies which are entirely restricted to this plant association: these are *Danaus affinis* (F.), *Tenaris horsfieldii* (Swains.), *Rapala drasmos* H. H. Drc. and *Suastus gremius* (F.), all of which are very rare in collections and by no means common where they occur.

Distribution frequencies of Malayan species of butterflies.

From the figures for relative abundance given in the tables on previous pages, it is very evident that the Malayan species of butterflies are not equally common. In fact, the frequency distribution of the species collected by me under the conditions detailed on page 107 resembles the "hollow curve" of Willis (1922, *Age and Area*) (*vide* Table XI). The numerically largest group comprises

TABLE XI.

Distribution frequencies of species collected in Malaya from 1927 to 1932.

S	n	S	n	S	n	S	n
304	0	10	19	3	38	1	59
118	1	10	20	3	39	2	60
74	2	11	21	1	40	1	64
44	3	5	22	1	41	1	66
24	4	3	23	2	42	1	68
29	5	3	24	1	43	1	70
22	6	5	25	1	44	4	71
20	7	4	26	4	45	1	76
19	8	8	27	2	46	1	84
20	9	3	28	1	48	1	89
15	10	3	29	2	49	1	92
12	11	2	30	3	50	1	93
14	12	5	31	1	51	1	100
6	13	4	32	2	52	1	105
12	14	7	33	1	53	1	108
6	15	4	34	4	54	1	119
9	16	5	35	1	55	1	141
9	17	3	36	5	56	1	147
6	18	3	37	2	58	1	194

The figures in the columns headed S show the number of species of which n specimens were obtained.

Thus, 620 species were represented by the 9031 specimens collected. The species of which 194 specimens were obtained was *Eurema hecabe* (L.).

species of which no specimens were obtained; next follow species represented by single examples, then species with 2 specimens and so on. If the values given in Table XI are converted into their respective logarithms, it is found that, between $n = 1$ and $n = 24$, the plot closely approximates to a straight line, and the relation between S and n is expressed by the equation :—

$$S = C/n^m$$

where m and C are constants.

The results for each Rhopalocerous family taken separately show the same exponential distribution, but it is obvious that, had collecting been continued, with a consequent increase in the number of species represented, the frequency diagram would show a maximum which would gradually rise as more and more specimens were obtained.

As this mathematical aspect of the distribution of species has an important bearing on the matter of collecting biological material in equatorial countries, it is hoped that it may be possible to return to the subject on a future occasion.

Summary.

It has been found that an area in the north-west corner of British Malaya (here termed " Kedawi " for convenience of reference), and the east coast islands of the Tioman group constitute two specialised faunistic areas characterised by the presence of species not otherwise found in Malaya and by geographical races which are distinct from the corresponding forms from Malaya proper. The boundary line separating " Kedawi " from Malaya proper is in the neighbourhood of the Kedah River, and Ridley found this same line constituted the northern limit of the flora of Malaya proper. Ridley postulated a former sea channel where Kedah now stands, but a more probable explanation is that, while the present Malay Peninsula has undoubtedly been separated from the asiatic mainland since the advent of the present species of butterflies, this separation occurred north of Kedah and the southward spread of insects and plants has been obstructed by a barrier which is largely climatic. Evidence put forward in the present paper shows that the union or reunion of Peninsular Malaya with the asiatic mainland was effected after the severance of Malaya from Sumatra and the other Large Sunda Islands.

The distribution of Malayan Rhopalocera has been studied quantitatively with respect to abundance, altitude, plant association and extra-Malayan distribution. The majority of the Rhopalocerous species in Malaya proper are of Malaysian origin, probably arising when Malaya, Sumatra, Borneo and Java were united to form the continent of Sundaland, but about one-tenth of the total have reached Malaya from the north after the separation of Malaya from Sumatra : these latter species are comparatively rare and largely confined to the mountains. On the other hand, the most abundant species in Malaya are those with the most extensive extra-Malayan distribution : a large proportion of these widespread insects are characteristic butterflies of secondary growth plant associations, and the recolonisation of the Krakatau Islands has been largely effected by butterflies thus characterised.

I should like to take this opportunity of expressing my thanks to Dr. Helen M. Muir-Wood and to Dr. F. E. Zeuner for much helpful criticism during the preparation of this paper.

GEOLOGY, CLIMATE AND FAUNAL DISTRIBUTION IN THE MALAY ARCHIPELAGO

By F. E. Zeuner, Ph.D., F.G.S., F.Z.S.

In his most valuable paper on the distribution of the butterfly fauna of Malaya, Dr. Corbet states that the extreme north-west of British Malaya (North Kedah, Perlis and the Langkawi Islands) differs remarkably from the remainder of the Peninsula (called Malaya proper), the number of Burmese species being proportionately much larger and there being a number of species occurring in races distinct from the forms from Malaya proper. The fauna of the Langkawi Islands is even more highly differentiated than that of the adjacent mainland, but in view of the common features the entire area is considered as a unit, which is called Kedawi. It is evident that some factor, or factors, has set a limit to the further extension of the Kedawi fauna into Malaya proper, and such factors can either prevail at the present day, or have acted in the immediate past, *i.e.* the Pleistocene.

An even more marked differentiation has been observed on Tioman Island, off the east coast.

The taxonomic differences involved are without exception of less than generic value. It is unlikely, therefore, that the factors which might have influenced the evolution and geographical restriction of species and subspecies date further back than the late Tertiary, and the great majority of forms are most probably not older than the Pleistocene.

In connection with the differentiation of new varieties and their (apparent or real) consolidation as subspecies or species, the following main factors have to be considered.

(1) Geographical changes: connections and disconnections of parts of the Archipelago:

(1a) due to tectonic movements,
(1b) due to fluctuations of the sea-level.

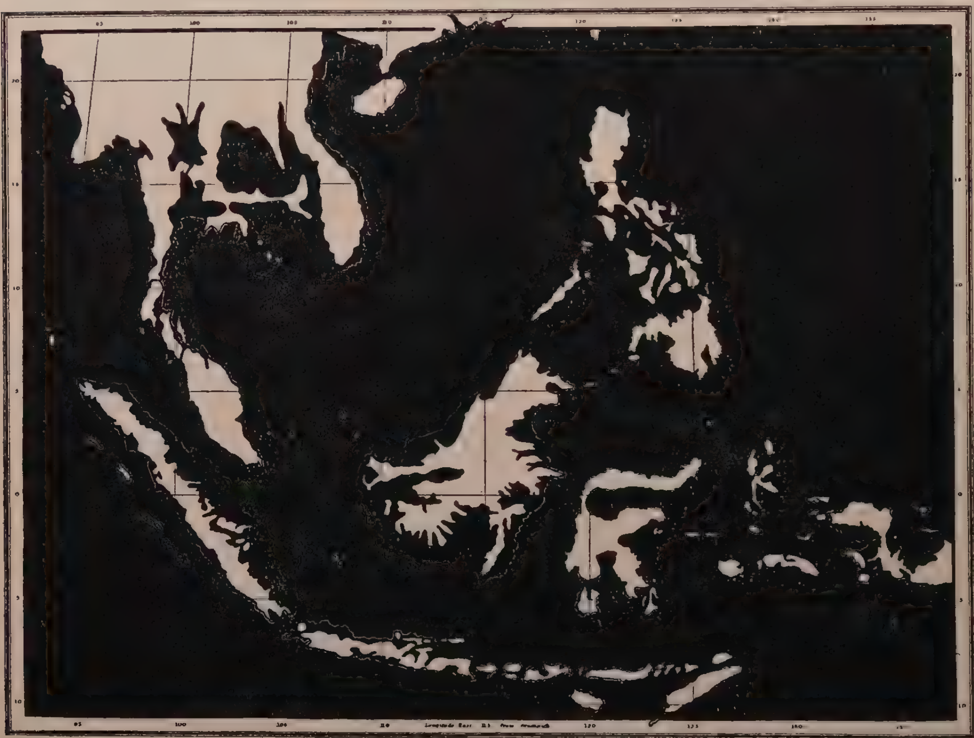
(2) Geological strata and soils.
(3) Climatic conditions, past and present:

(3a) Climatic fluctuations during the Pleistocene,
(3b) Present-day climatic conditions.

(1a) The Malay Archipelago consists of a stable block, Sundaland, comprising the Peninsula, eastern Sumatra, part of the north coast of Java, Borneo and the sea basin between them and, on the other hand, the outer zone of the mountains of Sumatra, Java, the Lesser Sunda Islands, Celebes, etc. The outer zone, much of which is volcanic, is in a state of tectonic activity (Brouwer, 1925; Scrivenor, 1941), and considerable earth movements have taken place here during and after the Tertiary. There is plenty of evidence that they still continue. It is impossible, however, to account for these movements in the attempted reconstruction of the Pleistocene conditions which follows. They have to be borne in mind as a possible source of error but, fortunately, they hardly affect the comparatively stable block of Sundaland.

(1b) It is known that, since the beginning of the Pleistocene, the sea-level has undergone repeated fluctuations. These were chiefly due to the formation of large ice-caps in the higher latitudes, resulting in a drop in sea-level, and to

the more or less complete melting of the ice during the interglacials and after the Last Glaciation, resulting in high sea-levels. The high sea-levels of the earlier phases were higher than the present (as much as 100 m. in the Sicilian phase, earliest Pleistocene). The standard succession for the phases of high and low sea-levels has been worked out in the Mediterranean, but evidence shows that it applies also to other parts of the earth, including South Africa and Australia (for details, *see* Zeuner, *Geology Prehistory and Time*, in preparation). One is justified, therefore, in assuming that the same or very similar levels apply to the Malay Archipelago, though local evidence is still scanty.



1

Fig. 1.—Submergence of the Malay Archipelago by 100 m. (330 ft.). Based on the 100-m. contour and various levels given in recently published maps, chiefly from the Atlas van Tropisch Nederland, 1938. A submergence of about 100 m. occurred in the earliest Pleistocene (Sicilian phase); the sea-levels of later phases were not so high (Milazzian 60 m., Tyrrhenian 32 m., Monastirian 19 and 7·5 m.). The chart represents the maximum of disconnection in the Archipelago and, therefore, the maximum of marine barriers to faunal and floral migration.

Evidence for former *high* sea-levels along the coast of Malaya proves that the sea once stood at least 50 ft. higher than at present, whilst certain observations suggest as much as 200 or 300 ft. (Scrivenor, 1931), figures which are in keeping with the Mediterranean evidence. A sea-level only 50 ft. higher than the present would submerge considerable portions of Sumatra and Borneo, and part of the coastal plain of the Peninsula. A submergence of about 300 ft. would produce much greater modifications (fig. 1). The Peninsula would be severed from the continent of Asia by a fairly broad sea-channel approximately

between Trang and Bandon in Siam (now used by a railway). In addition, at least two further, narrow, channels may have been formed, one across the Isthmus of Kra (76 m). and one in northern Perlis (92 m. at Padang Besar). It is of course not strictly permissible to transfer the present-day topography to earlier phases of the Pleistocene, since erosion and deposition cannot be taken into account. One cannot be certain therefore whether narrow gaps like those of Kra and Padang Besar were sea-channels or not, but there is a possibility of it having been so. Moreover, other such gaps are bound to be discovered as the work of the cartographers proceeds in these little-known regions. Thus, it is likely that, in the earliest Pleistocene and possibly later, during the phases of high sea-level, the Malay Peninsula formed a chain of islands, with Malaya proper as the largest member.

2

FIG. 2.—Maximum amount of land-exposure during the Pleistocene phases of low sea-level. 200-m. depth-line used, the 100-m. and 70-m. lines not being at present available for the entire area. The 200-m. and 100-m. lines are, however, close to one another almost everywhere, so that the difference is negligible in small-scale charts. Submarine river-channels based on Dutch maps and papers. Material: Atlas van Tropisch Nederland, 1938, and other charts and maps chiefly of Dutch origin.

Evidence for a considerable *drop* in sea-level at a certain stage (or stages) of the Pleistocene is abundant in the Archipelago (Molengraaff, 1921, 1930; Umbgrove, 1930) and points to a coastline of about −100 m. (Umbgrove) or possibly a little less (Daly, Molengraaff). The river-channels of Sumatra and Borneo, which have been traced beneath the present sea-level in connection with mining operations, form part of a large system that discharged into the

China Sea near the island of Great Natuna. Unfortunately, no charts are at present available for tracing the —100 m.-line for the whole archipelago and the —200 m.-line had to be used in fig. 2 instead. The two lines are close to one another wherever this can be ascertained, so that the general picture of distribution of land and sea at a sea-level of —100 m. is very nearly the same as at —200 m. A low level of —100 m. has been claimed for the Last Glaciation. Some workers, however, are inclined to assume a drop to —200 m. for the earlier glaciations. Fig. 2 clearly shows the compact mass of Sundaland. It also shows that the Wallace Line persisted through a phase of low sea-level, as did the Weber Line separating the Australian block from the Archipelago.

In interpreting faunal relations by means of the maps, figs. 1 and 2, it has to be remembered that conditions of this type alternated repeatedly during the Pleistocene.

(2) The rocks of any area influence, directly or indirectly, flora and fauna. In the case of butterflies, the soils developed on certain types of rock will determine the character of the flora on which, in turn, the caterpillars depend for food. From this point of view it is important that Langkawi, Perlis and north Kedah (and probably adjacent Siam also) contain considerable areas of limestone (Scrivenor, 1931). It will be necessary to return to this point when discussing the present climate.

(3a) Since the several glaciations which occurred during the Pleistocene in the temperate regions modified the climates of the non-glaciated regions, one would expect to find that the Malay Archipelago also was affected. Scrivenor (1941) holds that the climate was cooler during the Pleistocene (*i.e.* in certain phases) and relies on evidence of a former greater glaciation of New Guinea. However much or little there might have been of a cooling of the atmospheric climate, the lowering of the sea-level must have enlarged the areas of mountain climate. Conversely, a rise of sea-level might have favoured the formation of isolated mountain faunas. Repeated climatic fluctuations undoubtedly occurred in the Malay Peninsula during the Pleistocene and influenced fauna and flora, but our knowledge regarding this area is still entirely theoretical.

(3b) There remains the question of the extent to which the present-day climate might limit the distribution of species or subspecies and give the impression that there was, in the past, a geographical barrier of some sort. It is essential to examine this point because of the peculiar character of the Kedawi fauna as established by Dr. Corbet. In the tropical zone, slight differences in temperature are less likely to affect butterflies than is the occurrence of a dry season.

There are several types of climate in British Malaya (Stewart, 1930), some with one fairly distinct drier season, and some with two comparatively dry seasons. From the present point of view it does not matter when these occur so long as they are pronounced. For this reason, I have calculated a *seasonal index*, expressing the rainfall of the driest month in per cent of that of the wettest. The material was provided by Stewart's tables. The index proves to be lowest for climates with a pronounced dry season.

It is conceivable, however, that the *total annual rainfall* at any one place is so high that even the driest month is still damp enough to prevent an influence on the flora and fauna from becoming noticeable. In fig. 3, therefore, the index is plotted against the annual total of rainfall for each of the 55 stations given by Stewart.

The result is most illuminating. Whilst " Malaya proper " constitutes a comparatively uniform region with the rainfall of the driest month being one-third to two-thirds of the wettest, two areas with pronounced dry seasons are

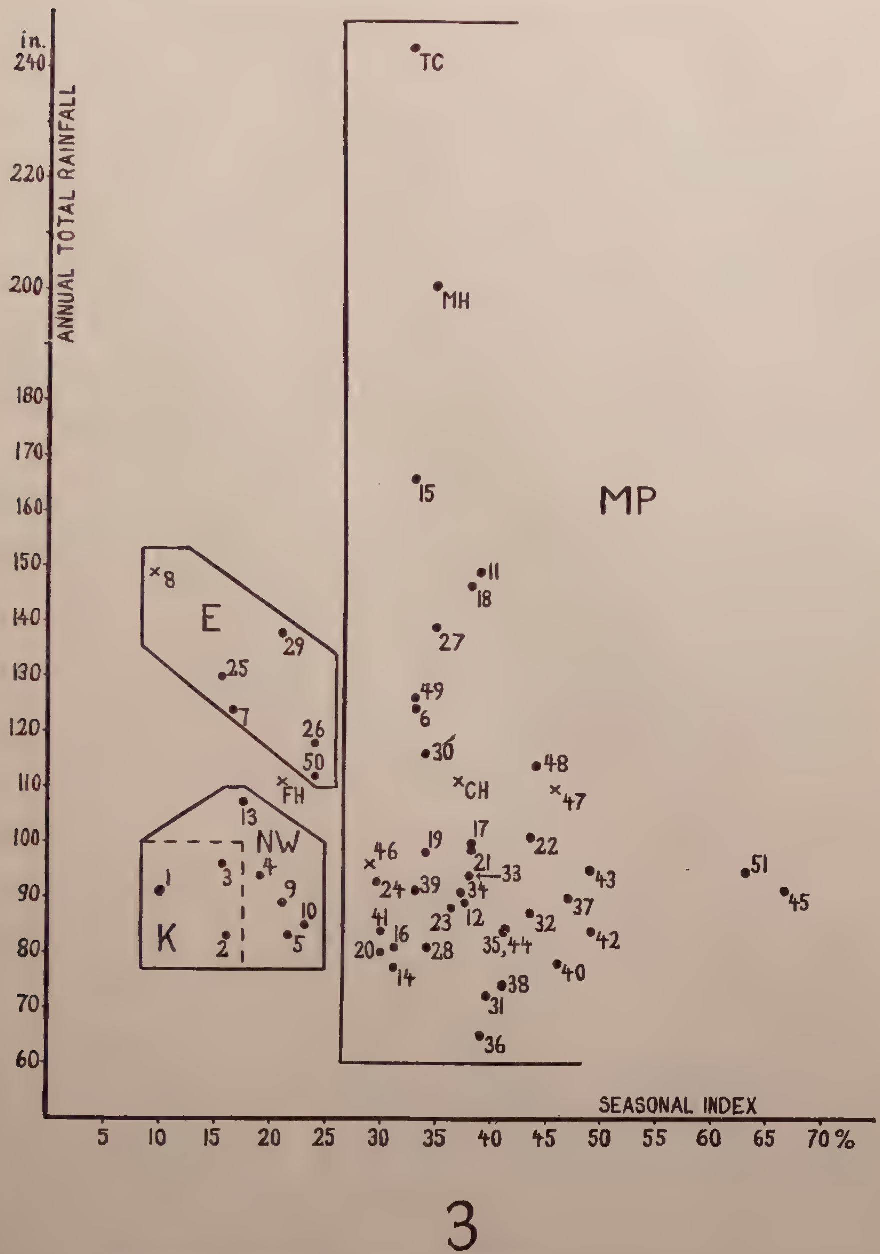


Fig. 3.—The seasonal variation of rainfall in British Malaya. Seasonal index (driest month : wettest month) plotted against annual total. Dot : Station with 10 or more years' record. Cross : Station with less than 10 years' record. Numbers of stations as in Stewart, 1930 : 1. Langkawi, 2. Perlis, 3. Alor Star, 51. Singapore. MP : Malaya proper. E : East coast. NW : north-west of British Malaya. K : Kedawi region of Dr. Corbet. This has the greatest seasonal differences. Based on tables in Stewart, 1930.

revealed. One is the east coast; it is not of interest in this context. The other is the north-west corner of British Malaya, including Dr. Corbet's Kedawi. This north-west area is not the driest part of British Malaya, since the annual total is, in the average, much the same as in Malaya proper, but it has the greatest seasonal extremes. The driest month receives from one-tenth to less than one-quarter of the rainfall of the wettest month. Within the north-west area, the three stations belonging to Kedawi (1. Langkawi, 2. Perlis, 3. Alor Star) are, in turn, the most extreme, and the absolute extreme is represented by Langkawi Island. These conditions indicate an approach to the climate of Tenasserim, Burma proper, continental Siam and Indo-China, where for instance at Tavoy, Rangoon, Bangkok and Saigon at least one month without any rainfall is encountered. If one now recalls that limestone covers considerable areas in Kedawi and that limestone everywhere accentuates dryness because of its permeability, it is easy to understand that many plants and insects of the Burmese sub-region were able to extend their area as far south as Kedawi but not farther into Malaya proper. It is highly probable, therefore, that the southern limit of the Kedawi fauna is, at present, climatic.

This result is of more than local significance, since it has been suggested more than once (most recently by Setchell, 1930) that the eastern boundary of the Malaysian sub-region (the Wallace Line) also is not merely geographical, but partly determined by the climate which, from Lombok eastwards, shows a very pronounced dry season (seasonal index for Kupang, Timor, 0). In Java, the transition from the typical Malaysian climate to the climate with a dry season may be observed. Buitenzorg is in total rainfall and seasonal index (51) similar to many stations of Malaya proper, but in Batavia, the seasonal index is only 9, and in Pasuruan, 2. This, in conjunction with its geographical position on the south-eastern edge of Sundaland, explains the comparatively great difference of the Javanese fauna from that of Sumatra, Borneo and the Peninsula.

Thus, it appears that the Malaysian sub-region with its rain-forest climate is at the present day bordered in the north and in the south-east by areas with a climate with pronounced dry seasons. The transition from one type of climate to the other coincides in both cases with geographical obstacles to migration: in the north, the bottleneck of the northern part of the Peninsula, in the south-east, the sea channel between Bali and Lombok. The present-day conditions thus explain very well why the uniform character of the Malaysian fauna is being maintained.

During the Pleistocene, conditions similar to those of the present day are likely to have prevailed during the interglacial phases of high sea-level. At certain phases, the Peninsula may even have been detached completely from the Asiatic continent (fig. 1). Conditions were even less favourable for faunal migration and intermingling than they are now. On the other hand, the isolation of Malaya proper, Sumatra, Borneo and Java from one another and from the continent must have favoured the evolution of geographical races.

During glacial phases, the sea-level was lower than at present, and the islands were connected by lowlands traversed by rivers. Each time this happened the faunas of Malaya, Sumatra, Borneo and (to a minor extent) Java met and mingled in these lowlands. This must have contributed greatly to maintaining the uniformity of the Sundaland fauna. The climatic character of these lowlands is not likely to have been very different from that of the tropical rain forest at any time during the Pleistocene. These lowlands are traversed by the equator and must always have been within the equatorial belt

of ascending air, even if the temperature was at times somewhat lower than now.

During the low sea-level phases, Sundaland was in broad connection with the Asiatic continent (fig. 2), and exchange of faunal elements was then easier than at other times. The mountainous nature of Burma, southern China and Indo-China, however, must have presented a barrier to many species of the rain-forest fauna, and in addition it is highly probable that the climate of Further India as a whole differed from that of Sundaland just as much as does now the climate of the Archipelago from that of Burma and Indo-China, so that the sub-regional character of the Malaysian fauna was largely maintained. The eastern limit to which the Sundaland fauna could expand without encountering a sea-channel, was Palawan, Borneo and Bali. In the south-west, the Mentawi Islands were separated from Sumatra by a wide sea-channel (except near Batu), but Nias only by a very narrow sea-passage. This explains why the fauna of Mentawi differs more from that of Sumatra than does the fauna of Nias. This is a typical case of geographical differentiation, in which the climate plays no recognisable part.

Another very striking case of geographical isolation without a recognisable influence of the climate is that of Tioman Island, studied by Dr. Corbet. It lies some distance off the east coast of Malaya in a shallow sea, and is topped by a mountain 3400 ft. high. While the sea-level was high (as at present), Tioman was completely severed from Malaya, and an island mountain fauna developed which now contains a surprisingly high number of species and subspecies confined to the island (42% among the butterflies, found by Dr. Corbet). When the sea-level was low, Tioman was linked with Malaya proper by lowlands which still presented a barrier to an exchange of mountain species and races between Tioman and Malaya, so that the peculiar character of the island fauna was largely preserved even during the phases of low sea-level.

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Book Notice.

Insect Pests of stored grain and grain products. Identification, habits, and methods of control. By R. T. Cotton. 8vo. Minneapolis, Minnesota (Burgess Publishing Co.), 1941. pp. 242, 93 figs. Price $3.

This book is printed by offset lithography in imitation typewriting, the figures, including photographs, being reproduced with the text. The volume is bound by a metal hoop threaded through a series of holes linking the single leaves on which the letterpress is printed.

The author is Senior Entomologist at the United States Bureau of Entomology and Plant Quarantine, and many of the figures are reproduced from publications of the Department. The eleven chapters are entitled: Insect pests of stored grain and milled cereals; Controlling stored grain insects on the farm; Control of insects in grain stored in elevators and warehouses; The insect problem in flour mills; Practical control methods in the mill; Protecting flour after manufacture; Fumigants and fumigation; The common fumigants; Flour mill and warehouse fumigation; Fumigation in atmospheric vaults and vacuum chambers; Heat sterilization in the flour mill.

The book is a handbook to the whole subject of controlling insect pests of stored grain and grain products. It is noteworthy that the most effective measures described are fumigation by one or other of the poison gases and some of the illustrations of men at work in their gas-masks are strangely familiar to the present-day reader in Europe.

Stress is laid on the desirability of preventing infestation so far as possible since, in the case of stored products, prevention is certainly better than cure.

The publishers ask that orders for the book from abroad should be accompanied by a remittance, when the book will be sent post free.

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